

Relationships between body size, wing morphology, and perch height selection in a guild of Libellulidae species (Odonata)

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ABSTRACT

Ten common libellulid species perch along the shoreline of lakes and ponds in South Carolina, USA. We collected individuals at five ponds throughout summer 2005, weighed them in the field, and calculated wing loading ($N \cdot m^{-2}$) and wing aspect ratios from digital photographs. We measured the perch-height preferences of these species in 'low perch' (10, 20, 30, and 40 cm) and 'high perch' (20, 40, 60 and 80 cm) experiments. Flywheel anemometers recorded wind speeds at each perch height. Species differed significantly in mean body mass, spanning nearly an order of magnitude from *Perithemis tenera* (67 mg) to *Libellula vibrans* (633 mg). There were also significant differences in wing morphology that correlated with mean mass; larger species had greater wing loadings and greater wing aspect ratios than smaller species. Species also differed significantly in their perch-height preferences in both experiments, in a manner correlating with body mass and hind-wing aspect ratios. *Erythemis simplicicollis* and *P. tenera* preferred short perches, *Celithemis fasciata*, *Pachydiplax longipennis* and *Plathemis lydia* used perches of intermediate height, and *Libellula auripennis*, *L. cyanea*, *L. incesta*, *L. luctuosa*, and *L. vibrans* preferred the tallest perches. Because mean wind speed and maximum wind speed also increased with perch height, larger species may prefer taller perches to experience greater wind speed and generate more compensatory lift to offset their larger wing loadings. However, it is also possible that correlations between body mass and perch height are the result of large species competitively restricting smaller species to lower perches.

INTRODUCTION

Body size is a fundamental determinant of a species' ecology. Differences in body size or body proportions correlate with home range, species range, rates of nutrient acquisition, metabolism, and reproductive strategies (Peters 1983; Elser et al. 1996; Brown et al. 2004). Body size and wing proportions are particularly important for flying animals because these characteristics influence critical aspects of

flight dynamics such as lift, drag, speed, and maneuverability (Norberg 1995; Lindhe Norberg 2002). In birds and bats, there are significant differences in body size and wing characteristics between species that exploit different ecological niches (Fleming 1986; Findley 1993; Landmann & Winding 1993; Norberg 1994; Hertel & Balance 1999). In odonates, the structural and behavioral elements of flight, itself, has received the most attention. This research has revealed extraordinary aspects of odonate flight, from the functional significance of the pterostigma (Norberg 1972), wing venation, and corrugation (Wootton 1981, 1991), to the importance of stroke dynamics such as stroke amplitude, stroke frequency, angle of attack, and the recovery stroke in generating speed, power, and lift (Ennos 1989; Rüppell 1989; Wootton 1991; Grabow & Rüppell 1995; Wakeling 1997; Wakeling & Ellington 1997a-c).

While the mechanics of odonate flight have been impressively described, studies on the potential ecological significance of interspecific variation in body size and wing morphology have lagged. May (1981) reported significant morphological differences between the major guilds of 'perchers' and 'fliers' with fliers having longer wings than perchers at a given body size. However, Wakeling (1997) found no significant differences in wing morphology between perchers and fliers in his study. Within the guild of perchers, there are several anecdotal accounts of larger species displacing smaller species from perches (Warren 1964; Williams 1976; Moore 1991). These interactions may not result in competitive exclusion from a habitat (Moore 1991), but they can result in resource partitioning to reduce the time and energy spent on defending perches from other species (Rehfeldt & Hadrys 1988; Worthen & Patrick 2004).

These studies suggest there are ecologically important morphological differences among odonate species. Also, these differences may correlate with patterns of perch-height use related to body size. Perching is an important behavior for male odonates; they can save energy (May 1984; Baird & May 1997) and thermoregulate (May 1976, 1978) while surveying territories for food (May 1984; Baird & May 1997), mates (Moore 1952; Ottolenghi 1987; Gorb 1995; Martens 2001), and competitors (Switzer & Eason 2000; Schultz & Switzer 2001). Because perch selection may have important consequences for energy budgets and reproductive success (Parr 1983; Wolf et al. 1997; Switzer 2002; but see Baird & May 2003), there should be strong selection for identifying and acquiring high-quality perches and defending them from competitors.

There is certainly strong evidence for aggressive competition for perches in several species of odonates (Lutz & Pittman 1970; Moore 1987; Schulz & Switzer 2001; Worthen & Patrick 2004), and it appears that perch height can be an important aspect of perch quality. Some species may partition perches with respect to perch height, with reproductive males displacing non-reproductives to less preferred perches (Eberhard 1986; Cordoba-Aguilar 1994). These intraspecific interactions may have important fitness consequences, although the effects of body size on male reproductive success is equivocal (for conflicting perspectives see Sokolovska et al. 2000; Thompson & Fincke 2002). Interspecific differences in perch heights have also been documented (Rehfeldt & Hadrys 1988; König 1990; Soeffing 1990; Worthen & Patrick 2004), and again, size effects are implied by anecdotal accounts of larger species displacing smaller species from perches (Warren 1964; Williams

1976; Moore 1991). Rehfeldt & Hadrys (1988) demonstrated interspecific partitioning of perch height between *Sympetrum flaveolum* (Linnaeus) and *S. sanguineum* (Müller), and Worthen & Partick (2004) demonstrated perch height partitioning resulting from interference competition between *Pachydiplax longipennis* (Burmeister) and *Perithemis tenera* (Say). This was an asymmetrical interaction, where the larger *P. longipennis* caused the smaller *P. tenera* to shift to shorter perches, with no reciprocal effect (Worthen & Patrick 2004). However, these are the only studies to examine the effects of interspecific competition on perch height selection, and neither explicitly considered the relationships among body size, wing morphology and perch height.

In this study, our goals were to: (1) describe ecologically important morphological differences among species in a guild of summer perching anisopterans; (2) describe differences in perch height selection among these species; and (3) determine whether differences in perch height selection were related to morphological patterns in any ecologically meaningful way.

MATERIALS AND METHODS

Experimental design

Five man-made ponds were selected in the piedmont of northwestern South Carolina, USA. Four sites were in Greenville County, SC, and one was in Union County, SC. Two ponds were sampled in the Blue Wall Preserve at the northeastern boundary of Greenville Co., ca 1.8 km south of the North Carolina border. The ponds were both ca 2 ha, and were ca 500 m apart. They were designated as 'Upper Blue Wall' (UB; 35°10'N, 82°15'W, alt. 403 m) and 'Lower Blue Wall' (LB; 35°10'51N, 82°15'W, alt. 380 m). The third pond, ca 1 ha, was on the Bunched Arrowhead Heritage Trust Preserve (BA), ca 15 km N of Greenville, SC (34°59'N, 82°22'W, alt. 303 m). The fourth pond in Greenville County was a 12 ha man-made impoundment on the campus of Furman University, designated 'Furman Lake' (FL; 34°55'N, 82°26'W, alt. 306 m). The fifth pond was a 15 ha impoundment off the Tyger River in Sumter National Forest, Union Co., SC (SF; 34°36'N, 81°37'W, alt. 108 m).

Each site was visited an average of once per week from 8 June through 14 August 2005, to observe the perch selection behavior of male anisopterans and to measure morphological attributes. After a day's observation was complete, individuals were collected by aerial net and body mass was measured in the field using an Ohaus® AV53 portable analytical balance (accuracy 0.001 g). After weighing, each individual in a species was uniquely marked with a sequence of colored dots on one wing. Individuals were marked to prevent weighing and measuring the same individual during the next sampling period, while also allowing for the possibility of recording perch events by uniquely marked individuals. However, no marked individuals were ever seen or recaptured in subsequent sampling weeks. Individuals were photographed in profile with a Konica Dimage Z3 digital camera. One voucher specimen of each species collected at each site was deposited in the Furman University Zoological Collection. All other individuals were immediately released

on site after their photographs were taken. The digital images were used to measure forewing and hindwing surface areas (SA) and wing lengths (L) using ImageJ software (Rasband 2005). Forewing and hindwing aspect ratios were calculated as: $L^2 \cdot SA^{-1}$. Wing loading was calculated as:

$$N \cdot m^{-2} = (9.807 \text{ m sec}^{-2}) \cdot (\text{mass in kg}) / 2 (\text{forewing} + \text{hindwing surface area in m}^2)$$

Perch selection preferences were described in two experiments. The first experiment examined preferences for a variety of 'low perches' (10-40 cm in height). Five perch stations, 5 m apart and 50 cm from the shoreline, were established at each pond. At each perch station, four wooden dowels (7.5 mm diameter) were positioned vertically, 10 cm apart, emerging above the water to heights of 10, 20, 30, and 40 cm. The order of the heights was randomized within each station. Perches were left at the sites between observations.

Each pond was visited at least four times (BA was visited six times) between 8 June - 21 July 2005; typically at weekly intervals. Upon arriving at a pond for an observation session, the dowel heights and distances from shore were adjusted to account for any changes in the water level of the pond. In addition, a 'wind station' was positioned between the second and third perch stations 50 cm from the shore, with four flywheel anemometers (Kestrel® 1000), attached to a stake at heights of 10, 20, 30, and 40 cm above the water surface. The flywheels were oriented perpendicular to the shoreline. During the one-hour observation period, we listed as many landings and departures as possible, noting the species, perch height, and station. By noting intervening departures, separate perch events could be tallied. Mean wind speeds and max. wind speeds were recorded after 30 min and 60 min; anemometers were reset after the 30 min recording.

During the low perch trials, we noticed that several species used the highest 40 cm perch almost exclusively. We became interested in knowing whether these species preferred 40 cm perches or would use taller perches if present. So, when low perch replicates were completed at a pond, we began a second experiment to

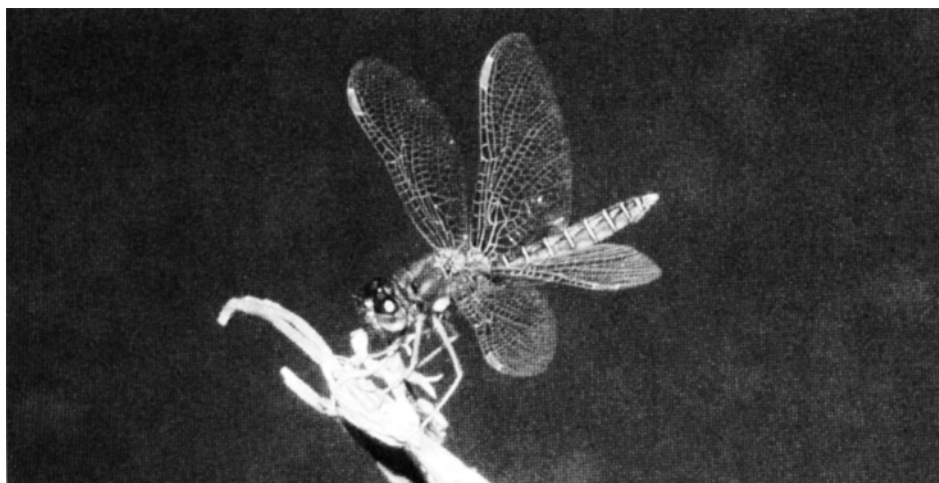


Figure 1: *Perithemis tenera* prefers short perches. Colgate campus, 15 July 1999; photo by Reinhard Jödicke.

examine the preferences of these species for a variety of 'high perches' (20-80 cm in height). Low perch dowels were replaced at each perch station with dowels that emerged 20, 40, 60, and 80 cm above the water surface. Again, perches were positioned 10 cm apart and 50 cm from shore at each station, and the five stations at each pond were 5 m apart. Four high perch replicates were conducted at each pond between 6 July - 14 August 2005, typically at weekly intervals. Observations and wind measurements were made in the same manner as in the low perch trials.

Data analyses

We observed males of 13 species perching on our dowels during the experimental trials. Three species were incidental visitors and were not included in the analyses: *Celithemis elisa* (Hagen), *C. eponina* (Drury), and *Libellula axilena* Westwood; they perched on only one day, at one site, across both experiments. Analyses were limited to the other 10 species: *Celithemis fasciata* Kirby, *Erythemis simplicicollis* (Say), *Libellula auripennis* Burmeister, *L. cyanea* Fabricius, *L. incesta* Hagen, *L. luctuosa* Burmeister, *L. vibrans* Fabricius, *Pachydiplax longipennis*, *Perithemis tenera*, and *Plathemis lydia* (Drury). Nine species were present in both low and high perch experiments. *L. vibrans* was only observed during the high perch trials, but it was observed on three different dates, at two sites, and perched more than 50 times. *P. tenera* was observed perching only once during the high perch trials, but its perch selection was consistent with its preference in earlier low perch trials and previous research (Worthen & Patrick 2004; Fig. 1). Differences among species in mean body mass, forewing aspect ratio, hindwing aspect ratio, and wing loading were compared with MANOVA, one-way ANOVA, and Tukey multiple comparison tests.

The independent perching behaviors of these 10 common species were described by limiting analyses to perch events where individuals perched alone within an array and had the full range of perch heights available for selection. Perch events were recorded without identifying individuals; we simply noted departures as well as perches and considered each perch as an independent event. Given the site fidelity of territorial males, many perch events in a given array, on a given day, were repeat visits by the same individual. However, the effect of an anomalous individual is dampened by the simultaneous observations of 5 arrays, across 4-6 replications, across 5 ponds.

Comparisons between species in perch use were made with χ^2 tests of independence. Mean perch height in low perch and high perch trials were also calculated for each species, and were compared with mean body mass, wing loading, and forewing and hindwing aspect ratios using Spearman rank correlations. The effect of 'perch height' on mean wind speed and maximum wind speeds were analyzed with ANCOVA tests. Given the large daily variation in wind speed, and the fact that differences among treatments should correlate with daily wind speed – no difference when the air is still, greater variation as wind speed increases –, mean daily wind speed, averaged across all heights during that recording interval, was included as a covariate. Tukey mean comparisons comparing mean and maximum wind speeds across height treatments were performed, but they do not include the relationship with the covariate. So, ANOVA and Tukey mean comparisons were used to analyze and describe the differences (residuals) in mean and maximum wind speeds from the daily mean across height treatments.

Table 1. Mean comparisons among males of ten libellulid species for mass [mg], wing loading [$N \cdot m^{-2}$], forewing aspect ratio, and hindwing aspect ratio. Means were significantly different among species (MANOVA, see text). Species are listed in order of increasing mass to facilitate mean comparisons. Within each column, means followed by the same letter are not statistically different (Tukey's post-hoc multiple comparison tests, $p = 0.05$). Wing loading and aspect ratios are significantly correlated with mean mass; see text.

Species	<i>n</i>	Mass [mg]	Wing loading [$N \cdot m^{-2}$]	Fw aspect ratio	Hw aspect ratio
<i>Perithemis tenera</i>	12	67.7 \pm 10.2 a	1.63 \pm 0.15 a	4.16 \pm 0.10 a	3.27 \pm 0.12 a
<i>Celithemis fasciata</i>	14	123.1 \pm 10.8 b	1.50 \pm 0.19 a	4.72 \pm 0.14 b	3.70 \pm 0.12 c
<i>Pachydiplax longipennis</i>	54	196.3 \pm 39.4 c	2.14 \pm 0.13 b	4.93 \pm 0.14 c	3.76 \pm 0.12 cd
<i>Erythemis simplicicollis</i>	29	214.9 \pm 27.4 c	2.17 \pm 0.15 b	5.00 \pm 0.19 cd	3.91 \pm 0.08 e
<i>Libellula cyanea</i>	25	286.2 \pm 36.1 d	2.39 \pm 0.27 bc	5.00 \pm 0.29 cd	3.86 \pm 0.09 de
<i>Libellula incesta</i>	40	395.5 \pm 50.6 e	2.63 \pm 0.26 cd	5.39 \pm 0.13 e	4.24 \pm 0.09 f
<i>Plathemis lydia</i>	15	406.1 \pm 45.9 e	3.73 \pm 0.42 e	4.57 \pm 0.08 b	3.54 \pm 0.07 b
<i>Libellula auripennis</i>	1	437.0	2.60	4.92	4.02
<i>Libellula luctuosa</i>	21	442.6 \pm 57.3 e	2.36 \pm 0.22 bc	5.14 \pm 0.12 d	3.79 \pm 0.13 cde
<i>Libellula vibrans</i>	3	623.3 \pm 28.9 f	2.74 \pm 0.25 d	5.68 \pm 0.06 f	4.29 \pm 0.11 f

RESULTS

Morphological differences among species

Differences among species in mean mass, mean wing loading, and mean aspect ratios of forewings and hindwings were assessed with ANOVA, MANOVA, and Tukey mean comparison tests. Only nine species were included in these analyses; *Libellula auripennis* was not included because it was represented by only a single captured male. There was a statistically significant difference among these species in these morphological attributes (MANOVA Wilk's $\Lambda = 0.004$, $F = 83.64$, d.f. = 32, 742.85, $p < 0.0001$).

Species differed significantly in mean body mass (ANOVA $F = 233.11$, d.f. = 8, 204, $p < 0.0001$), spanning nearly an order of magnitude from *Perithemis tenera* (mean mass = 67.7 \pm 10.2 mg) to *L. vibrans* (623.3 \pm 28.9 mg; Table 1). *Celithemis fasciata*, *L. cyanea*, *L. vibrans*, and *P. tenera* were significantly different from all other species in body mass (Table 1). *Pachydiplax longipennis* and *Erythemis simplicicollis* were similar in size at roughly 200 mg, and *L. incesta*, *L. luctuosa*, and *Plathemis lydia* weighed near 400 mg (Table 1). *L. auripennis* also fell within this range (Table 1).

Species also differed significantly in mean wing loading (ANOVA $F = 91.44$, d.f. = 8, 204, $p < 0.0001$), mean forewing aspect ratio (ANOVA $F = 110.25$, d.f. = 8, 204, $p < 0.0001$), and mean hindwing aspect ratio (ANOVA $F = 150.16$, d.f. = 8, 204, $p < 0.0001$). Wing loading varied from $1.50 \pm 0.19 \text{ N}\cdot\text{m}^{-2}$ for the light-bodied, long-winged *C. fasciata* to $3.37 \pm 0.42 \text{ N}\cdot\text{m}^{-2}$ for the chunky, short-winged *P. lydia* (Table 1). *P. tenera* had the smallest forewing and hindwing aspect ratios (4.16 ± 0.10 and 3.27 ± 0.12 , respectively; Table 1). *L. vibrans* had the largest forewing and hindwing aspect ratios (5.68 ± 0.06 and 4.29 ± 0.11 , respectively; Table 1).

There were predictable positive correlations among these variables (Fig. 2). Mean mass was strongly positively correlated with wing loading (Spearman rank correlation, $r_s = 0.974$, $n = 10$, $p < 0.01$), forewing aspect ratio ($r_s = 0.600$, $n = 10$, $p < 0.05$), and hindwing aspect ratio ($r_s = 0.624$, $n = 10$, $p < 0.05$; Fig. 2). Forewing and hindwing aspect ratios were strongly positively correlated, as well ($r_s = 0.842$, $n = 10$, $p < 0.01$).

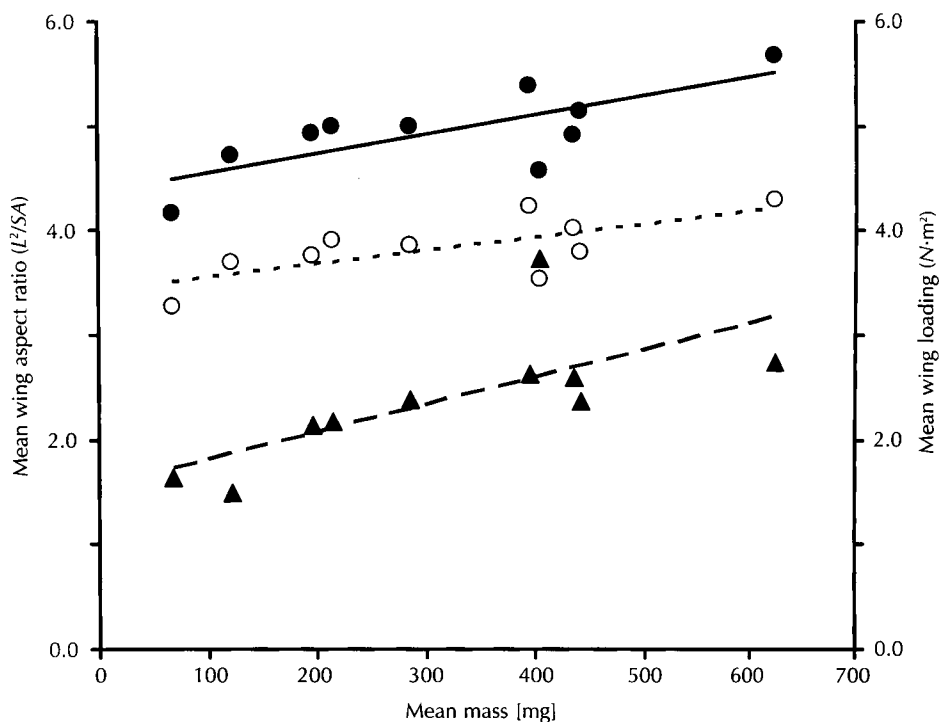


Figure 2: Relationships between mean mass [mg] of males of 10 common libellulid species and their mean forewing aspect ratio (● solid line), mean hind wing aspect ratio (○ dotted line), and mean wing loading (▲ dashed line). The three correlations with mean mass are statistically significant (Spearman rank correlations: forewing aspect ratio: $r_s = 0.600$, $n = 10$, $p < 0.05$; hind wing aspect ratio: $r_s = 0.624$, $n = 10$, $p < 0.05$; wing loading: $r_s = 0.974$, $n = 10$, $p < 0.01$).

Table 2. Frequencies of perch use by males of ten libellulid species in experiments using low perches (10, 20, 30, and 40 cm) and high perches (20, 40, 60, and 80 cm). Only perch events where individuals perched alone within a station were included. Species are listed in order of increasing mass to facilitate mean comparisons. Mean perch heights followed by the same letter signify species with similar distributions; sequential χ^2 tests of independence, $p = 0.05$ after a correction for multiple comparisons; see text. Mean perch height in both low perch and high perch trials is significantly correlated with mean mass and hindwing aspect ratio; see text.

Species	Low perch height [cm]	10	20	30	40	<i>n</i>	Mean	
<i>Perithemis tenera</i>		14	20	3	1	38	17.6	a
<i>Erythemis simplicicollis</i>		1	56	79	18	146	27.3	b
<i>Plathemis lydia</i>		0	12	28	39	79	33.4	c
<i>Pachydiplax longipennis</i>		2	15	176	492	685	36.9	d
<i>Celithemis fasciata</i>		0	0	12	58	70	38.3	d
<i>Libellula luctuosa</i>		0	0	1	14	15	39.3	d
<i>Libellula incesta</i>		0	1	7	128	136	39.3	d
<i>Libellula cyanea</i>		0	0	1	21	22	39.5	d
<i>Libellula auripennis</i>		0	0	0	16	16	40.0	d
<i>Libellula vibrans</i>		0	0	0	0	0	-	

Species	High perch height [cm]	20	40	60	80	<i>n</i>	Mean	
<i>Perithemis tenera</i>		1	0	0	0	1	20.0	a
<i>Erythemis simplicicollis</i>		19	10	0	0	29	26.9	a
<i>Plathemis lydia</i>		0	4	5	3	12	58.3	b
<i>Pachydiplax longipennis</i>		7	168	151	119	445	57.2	b
<i>Celithemis fasciata</i>		2	25	55	52	134	63.4	b
<i>Libellula luctuosa</i>		0	0	5	25	30	76.8	c
<i>Libellula incesta</i>		0	1	34	324	359	78.0	c
<i>Libellula cyanea</i>		0	0	0	6	6	80.0	c
<i>Libellula auripennis</i>		0	0	0	17	17	80.0	c
<i>Libellula vibrans</i>		1	0	0	11	12	75.0	c

Perch selection and relationships with morphology

The perch-height preferences of males from the 10 guild species were described by tabulating the frequencies of perch use when each species perched alone at a station and had access to all perch heights (Table 2). For both low and high perch experiments, the frequencies for each species were pooled across stations and across the five sampling sites, and total frequencies of perch height use were compared between species with pair-wise χ^2 tests of independence (Table 2). These tests were done in a sequential manner based on average perch height. For example, *L. auripennis* was compared with each species with a progressively lower average perch height until a statistically significant difference was found. In the case of low perch arrays, this occurred when *L. auripennis* was compared to *P. lydia* ($\chi^2 = 13.99$, d.f. = 3, $p < 0.05$ after a correction for 8 multiple comparisons, Table 3).

Perch use by *P. lydia* was then compared with the species with the next highest average perch height, *P. longipennis*. These species had significantly different patterns of perch use ($\chi^2 = 42.76$, d.f. = 3, $p < 0.05$ after a correction for 8 multiple comparisons, Table 2), so all species from *P. longipennis* to *L. auripennis* were bracketed as a group of species with similar patterns in perch use (Table 2). This method obscured some statistically significant pair-wise patterns that are resolvable because of large samples sizes; for example *P. longipennis* has a significantly different frequency distribution than *L. incesta* in a pair-wise test ($\chi^2 = 30.59$, d.f. = 3, $p < 0.001$). However this method is appropriately conservative for describing ordered patterns at the community level.

Using these sequential χ^2 analyses, *E. simplicicollis*, *P. tenera* and *P. lydia* differed from one another and all other species in perch height distributions in the low perch experiment, with mean perch heights of 27.3 cm, 17.6 cm, and 33.4 cm, respectively (Table 2). The other six species preferred the highest perches available (mean perch heights from 36.9 - 40.0 cm) and did not differ in their distributions of perch height use (Table 2).

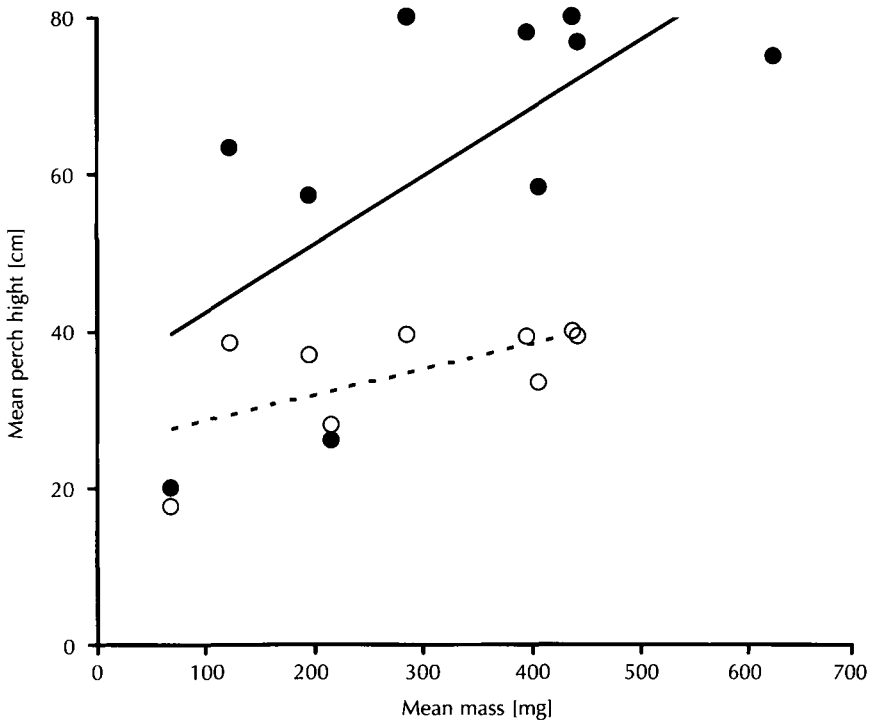


Figure 3: Relationship between mean mass [mg] and mean perch height [cm] for males from common libellulid species — perching in low perch (○ dotted line) and high perch (● solid line) arrays. Both relationships are statistically significant — low perch: $r_s = 0.611$, $n = 9$, $p < 0.05$; high perch: $r_s = 0.584$, $n = 10$, $p < 0.05$.

Table 3. Mean comparisons of average ('Avg.') and maximum ('Max.') wind speeds [$\text{m}\cdot\text{s}^{-1}$] recorded over 30 min intervals in low perch trials (10, 20, 30, and 40 cm perches; $n = 38$ for each height) and high perch trials (20, 40, 60, and 80 cm perches; $n = 34$ for each height). Raw data were analyzed with ANCOVA tests (ANC) that included the mean value for each interval as a covariate (see text for a justification). Although the height effects were significant in these ANCOVA, raw means do not reflect the effect of the covariate and were not significantly different in post-hoc tests (Tukey multiple comparison tests; means followed by the same letter are not significantly different, $p = 0.05$). To better describe this covarying height effect, ANOVA and Tukey tests were also performed on two derived variables; "Avg. differential": average wind speed – mean average wind speed for that interval. Likewise, "Max. differential": maximum wind speed – mean maximum wind speed for that interval.

Variable	Low perches [cm]	10	20	30	40	F	p
Avg. wind speed [$\text{m}\cdot\text{s}^{-1}$]		0.47 a	0.49 a	0.51 a	0.53 a	9.29 (ANC)	0.0001
Avg. differential		-0.03 a	-0.01 ab	0.01 bc	0.03 c	9.35	0.0001
Max. wind speed [$\text{m}\cdot\text{s}^{-1}$]		1.96 a	2.04 a	2.06 a	2.06 a	8.85 (ANC)	0.0001
Max. differential		-0.07 a	0.01 b	0.03 b	0.03 b	8.911	0.0001
Variable	High perches [cm]	20	40	60	80	F	p
Avg. wind speed [$\text{m}\cdot\text{s}^{-1}$]		0.52 a	0.56 a	0.57 a	0.59 a	16.36 (ANC)	0.0001
Avg. differential		-0.04 a	-0.01 b	0.01 b c	0.03 c	16.49	0.0001
Max. wind speed [$\text{m}\cdot\text{s}^{-1}$]		2.08 a	2.22 a	2.26 a	2.31 a	7.91 (ANC)	0.0001
Max. differential		-0.14 a	0.00 b	0.05 b	0.09 b	7.97	0.0001

In the high perch experiment, the species were distributed more evenly across this broader resource base. *E. simplicicollis* and *P. tenera* were again the species that preferred significantly lower perches than other species (mean perch heights of 26.9 and 20.0, respectively; Table 2), though these two species did not differ from one another in this experiment due to the single observation of *P. tenera* (Table 2). *P. longipennis*, *P. lydia*, and *C. fasciata* preferred perches of intermediate height (mean perch heights of 58.3, 57.2, and 63.4, respectively; Table 2); with distributions significantly higher than *E. simplicicollis* and *P. tenera* but significantly lower than the other species (Table 2). Finally, the four *Libellula* species preferred the tallest perches (Table 2).

The mean perch heights of these species were significantly correlated with mean mass and in both low perch ($r_s = 0.611$, $n = 9$, $p < 0.05$) and high perch ($r_s = 0.584$, $n = 10$, $p < 0.05$) experiments (Fig. 3). Mean perch heights were also significantly correlated with hindwing aspect ratio in both low perch ($r_s = 0.636$, $n = 9$, $p < 0.05$) and high perch ($r_s = 0.578$, $n = 10$, $p < 0.05$) experiments. Mean perch height did not correlate significantly with either wing loading or forewing aspect ratio ($p > 0.05$) in either experiment.

Wind speed at different perch heights

For both low perch and high perch experiments, average wind speeds [$\text{m}\cdot\text{s}^{-1}$] and maximum wind speeds [$\text{m}\cdot\text{s}^{-1}$] were recorded during two 30 min intervals of each observation period and were analyzed with ANCOVA tests (Table 3). There were a few intervals in each experiment in which an anemometer failed or turned off prematurely. No data from any of the anemometers were included in these cases. As such, although the design was balanced across perch heights, there were fewer samples than the complete experimental design would dictate (5 ponds \times 4 observation days/pond \times 2 wind intervals/day = 40 intervals per perch height). ANCOVAs were necessary to control for daily variation in wind speed. For instance, on a calm day, average and maximum wind speeds were uniformly low across all perch heights. However, on windier days, the increases were more pronounced at higher perch heights and the variation among recordings at different heights increased. As such, differences among raw means were obscured and confounded by the large daily variation in wind speed (Table 3). To control for these effects, the mean value of the four recordings taken during each 30 min interval were calculated and included as a covariate.

There was significant variation among perch heights in average wind speed and maximum wind speed, when daily wind speed was included as a covariate, in both the low perch and high perch arrays (Table 3). Average wind speed and maximum wind speed increased with increasing perch height in both the low perch and high perch trials, although mean comparisons among these raw means were not significantly different because of the large daily variation in wind speed (Table 3). To describe the effect of perch height on average and maximum wind speed while accounting for daily differences in wind speed, the difference between each observation and its daily mean were recorded and analyzed with oneway ANOVA tests (the effect of perch height on the "differentials" between each observation and the daily mean; Table 3). In both the low perch and high perch experiments, low perches had significantly lower differentials than higher perches for both average wind speed and maximum wind speed (Table 3). Values at low perches were consistently lower than the daily mean wind speed, while values at high perches within that array were consistently higher than the daily mean wind speed.

DISCUSSION

There were dramatic differences between species in mean mass, spanning nearly an order of magnitude. There were also significant positive correlations between body mass, wing loading, and wing aspect ratios, reflecting predictable, allometric changes in flight morphology. As mass increases, the increasing downward force must be offset by generating more lift by: increasing wing surface area, increasing air speed over the wing, and altering aspects of dynamic flight (wing angle, stroke rate, stroke recovery angle and speed, camber, etc.; Wakeling & Ellington 1997a, 1997c). Total wing surface area increased 5.5 fold, from 406 mm^2 in *Perithemis tenera* to $2,243 \text{ mm}^2$ in *Libellula vibrans*. However, mass varied nearly ten-fold from *P. tenera* to *L. vibrans*, so wing loading increased allometrically with increasing mass. This pattern is consistent with previous research (May 1981; Grabow & Ruppell 1995).

The allometric increase in wing loading means that other factors must generate compensatory lift in larger odonates. Increasing air speed is an obvious option for larger organisms with larger and stronger flight muscles, and flight speed does tend to increase with body size (Rüppell 1989). In terms of steady-state flight characteristics, true air speed increases with increased thrust, decreased drag, and increased headwind speed. Because drag decreases with increasing aspect ratio (longer, narrower wings), the significant positive correlation between body mass and hindwing aspect ratio in this guild may reflect a biomechanical adaptation of larger species to reduce drag.

In addition to morphological differences, these species also exhibited significant differences in perch height preferences. In the low perch experiment, *P. tenera* preferred low perches, *Erythemis simplicicollis* and *Plathemis lydia* preferred intermediate perches, and the remaining six species vied for the tallest perches. Most species showed a shift to higher perches when they were made available in the high perch experiment. However, while *P. lydia*, *Pachydilax longipennis*, and *Celithemis fasciata* increased their mean perch height to near 60 cm, the *Libellula* species exploited the 80 cm perches to a much greater degree and had mean perch height preferences equal or greater than 75 cm.

In both low perch and high perch experiments, the mean perch height preferences of these species correlated with mean mass and aspect ratio of the hindwing. Larger species perched at higher positions, on average, than smaller species. The correlations for the high perch experiment are even more significant if *L. vibrans* is excluded and the analyses only include the species found throughout the summer. In both experiments, *P. lydia* was the exception. It is a heavy species with the highest wing loading and low aspect ratios, but it perched at intermediate heights. May (1981) also noted its small wing area relative to body mass, and suggested that the short, strong wings may be advantageous for this species because it often perches on horizontal surfaces and must generate lift with short powerful strokes. It is also possible that the short, broad, pruinose white abdomen of mature males is under contradictory selective pressure as a sexual signal. Wakeling (1997) suggested this to explain the atypical wing morphology for the percher *Libellula depressa* Linnaeus, and the two species are strikingly similar. In addition, although odonate abdomens are not thought to contribute much aerodynamic lift (Wakeling & Ellington 1997a), it seems possible that the flexible abdomen of these species, which can be dramatically expanded laterally, might be exceptional in this regard. Nonetheless, even with *P. lydia* included in the analyses, the relationships between mean perch height and mean body mass and hindwing aspect ratios were statistically significant.

These perch selection patterns are also consistent with biomechanical efficiencies because mean and maximum wind speeds increase with perch height. Even over the fairly narrow range presented by the low perch heights (10–40 cm), there were small but statistically significant increases in wind speed with height, once average wind speed was taken into account. These differences became more pronounced when maximum perch height was raised to 80 cm, with maximum wind speed differentials between 20 cm and 80 cm perch heights of 0.23 m·s⁻¹. As mentioned above, lift increases with true air speed. When perching (thrust = 0), true air speed is equal to the headwind speed. Large species can compensate for their greater wing

loading by perching higher, where greater wind speeds will generate more lift. Of course, the benefits of increased lift at high perches should apply to all species. However, the benefits will be disproportionately great for larger species that experience a greater energetic cost of their disproportionately greater wing loading, and narrower drag-reducing wings. In addition, higher wind speeds may be destabilizing for very small species trying to remain stationary on a perch.

We conclude that perch height selection in this guild correlates with body mass. There are several biologically interesting hypotheses that may explain this pattern. This pattern may be a consequence of larger species perching at greater heights to exploit higher wind speeds. It should be possible to re-examine these data and test this hypothesis by seeing if perch height shifts with changes in wind speed. However, knowing that species compete for perch sites, it is possible that this pattern results from competitive interactions based on body size, or competitive interactions based on flight efficiencies that correlate with body size. And, although we limited our analyses to instances where individuals perched alone at a station, the effects of competition can not be discounted. Past competitive interactions might condition an individual to select a particular perch height, even when alone, that reduces the possibility of more interspecific encounters. It is intriguing to consider whether morphological differences drive perch selection or whether competition for perches drives evolutionary changes in morphology through character displacement. In the analyses reported here, all individuals within a species were pooled across sites. However, the sites differed rather dramatically in species composition, and it should be possible to test a number of hypotheses regarding character displacement by comparing the body sizes, flight characteristics, and perch selection of species in sympatry and allopatry at the site scale. In addition, we can test for community-level patterns such as species packing and orderly ratios in species morphology that are indicative of communities structured by interspecific competition (Simberloff & Boecklen 1981; Dayan et al. 1990; Simberloff & Dayan 1991). These analyses should clarify whether relationships between body size, wing morphology, and perch-height selection are consistent with predictions from competition theory.

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